

THE SWIMBLADDER OF THE TOADFISH (*OPSANUS TAU* L.)

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The swimbladder of the toadfish (*Opsanus tau* L.) offers a particularly favorable object for the experimental study of gas secretion. To provide a basis for physiological studies we describe here the structure of the swimbladder, its gas gland and its vascular supply. In addition, some physiological observations are presented. Further physiological studies of this species are reported elsewhere (Wittenberg, 1958).

Brief anatomical descriptions of the swimbladder of the toadfish are found in Tower (1908) and Rauther (1945). Greene (1924a) has studied a related species, *Porichthys*. Tracy (1911) presents some embryological and histological data. Tracy observed that the posterior chamber of the embryonic toadfish develops from the pneumatic duct, which secondarily loses its connection with the gut.

MATERIAL AND METHODS

Animals: Toadfish caught at Woods Hole were maintained in a shallow live car for several months before they were used.

Histological: After fixation in Bouin's fluid, histological sections were made and stained with azan (Romeis, 1948) or haematoxylin and eosin. The blood vessels were studied by injection of India ink into the coeliac artery. The injected specimens were fixed in Bouin's fluid and later cleared in benzyl benzoate.

Gas analyses: These were by the method of Scholander *et al.* (1955).

RESULTS

The swimbladder gases

In contrast to the majority of shallow-living marine fishes, the toadfish normally maintains a very high proportion of oxygen in the swimbladder gases. The oxygen ranges from 40 to 80 per cent and in most animals is about 50 per cent of the total gas. Similar high oxygen concentrations (maximum 88 per cent) have previously been observed in a related species, *Porichthys* (Greene, 1924b).

When forced experimentally to renew repeatedly the gaseous contents of the bladder, the toadfish is able to maintain the secretion of gas undiminished in rate and oxygen content. Thus in one experimental series the swimbladders of three animals were emptied every 24 hours for six days. During this time, each animal

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secreted a volume of gas equivalent to six times the volume of the swimbladder. At the end of the six-day period, the rate of secretion and the composition of the secreted gas remained unchanged. The newly secreted gas is characterized by an extraordinarily high proportion of oxygen which averages 90 per cent and may be as high as 96 per cent of the total gas. The proportion of carbon dioxide is low, about 4 per cent (Wittenberg, unpublished data). The ratio, argon to nitrogen, in the secreted gas is very high, 2.4×10^{-2} to 2.6×10^{-2} , and approaches the maximum which can be achieved by a mechanism of inert gas secretion proposed elsewhere (Wittenberg, 1958). These properties combine to indicate a very powerful development of oxygen transport in the gas gland of the toadfish, making this an animal of choice for experimental studies concerning oxygen transport.

The principal layers of the swimbladder wall

The external appearance of the swimbladder is shown in Figure 1. It is of the euphysoclist type (Rauther, 1922; Fänge, 1953). The wall may be described as formed of three layers, conveniently called tunica externa, submucosa and

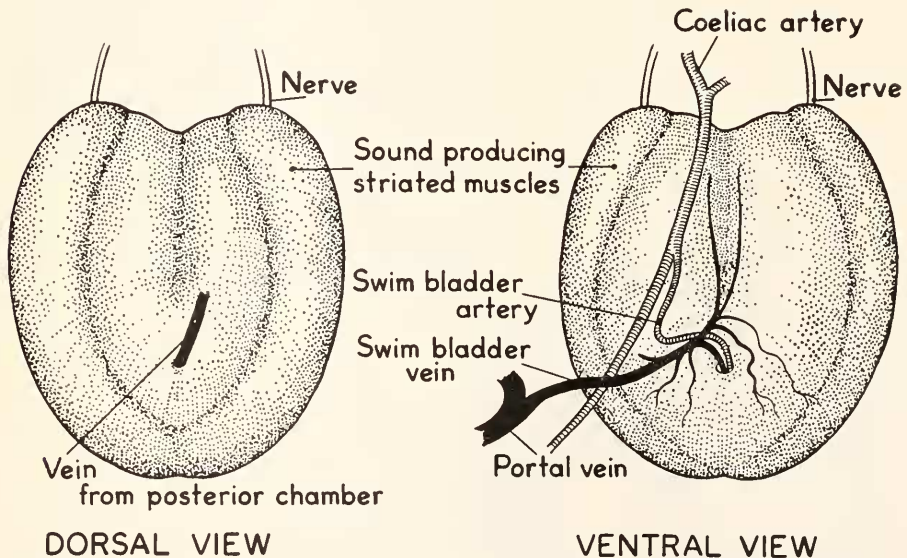


FIGURE 1. External view of the swimbladder of the toadfish seen in dorsal and ventral view. The nerve shown in the picture is the motor nerve to the striated sound-producing muscle. According to Tracy (1911) it is a branch of the first spinal nerve.

mucosa. The tunica externa is a tough, somewhat rigid external connective tissue capsule. Laterally this layer includes the sound-producing striated muscle masses (Figs. 1 and 2; compare with Rauther, 1945).

The submucosa consists of very loose fibrous connective tissue which allows a limited movement of the mucosa relative to the tunica externa. In fresh specimens it is possible to take advantage of the loose consistency of the submucosa to dissect away the tunica externa, including the striated muscle masses. The mucosa is

then revealed as a transparent, richly vascularized, sac composed of two chambers separated by a deep transverse constriction, the diaphragm (Fig. 2). The lumina of the two chambers communicate by a hole in the diaphragm (Fig. 2).

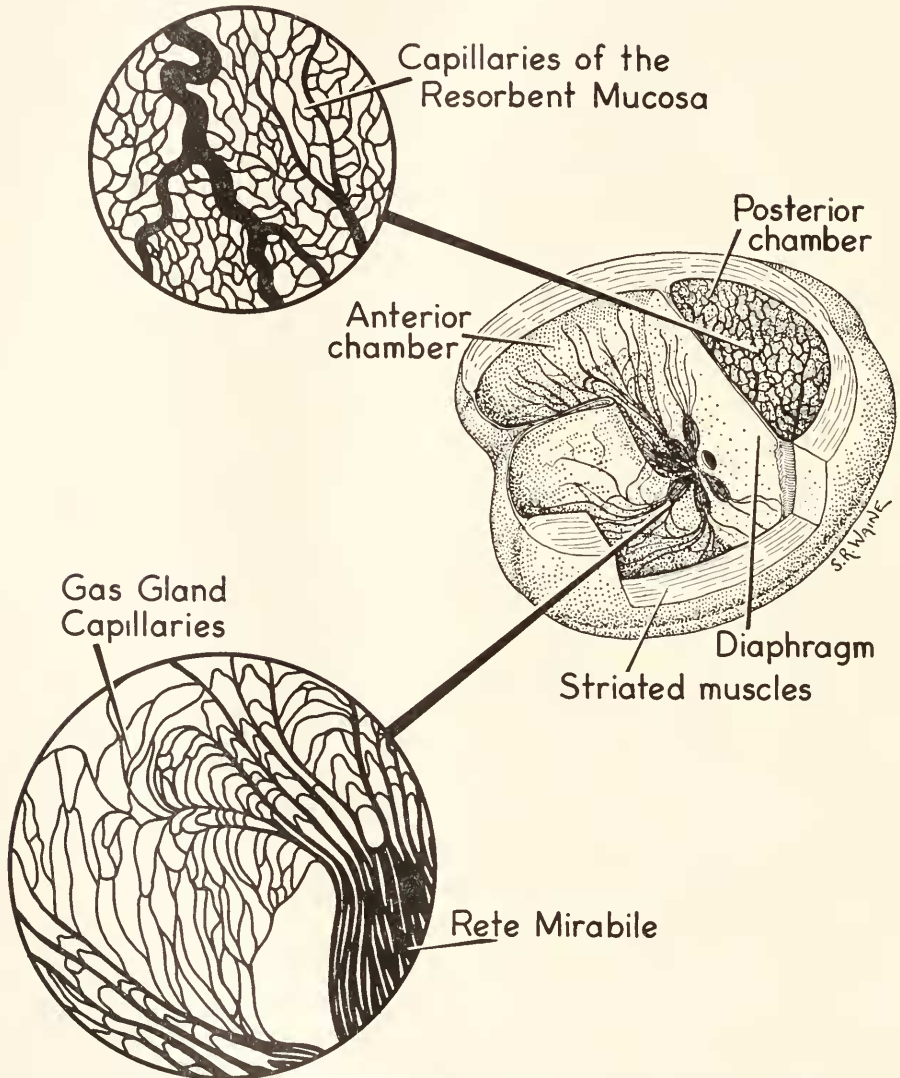


FIGURE 2. The swimbladder opened dorsally. Portions of the secretory mucosa and the resorbent mucosa are shown in higher magnification, in order to demonstrate the typical appearance of the blood vessels.

The anterior chamber, gas gland and retia mirabilia

The gas gland forms the epithelial lining of the floor of the anterior chamber and to a lesser extent it is developed on the anterior face of the diaphragm. Periph-

erally the gas gland is continuous with the cuboidal, apparently non-glandular, epithelium of the roof of the anterior chamber. The gas gland is most strongly developed and heavily folded within a few millimeters of the retia mirabilia (Fig. 3). At a distance from the retia the degree of folding dwindles rapidly and the glandular cells become smaller. The glandular epithelium is everywhere only one cell thick. The cells are columnar with a dense cytoplasm stained red by azan. An interesting feature of the gas gland cells is the position of the cell nuclei (Fig. 3). These are situated near the secretory lumen and not adjacent to the basal blood vessel as in most gland cells. This peculiar position of the nuclei has been noted by Woodland (1911) in the gas gland of the eel (*Anguilla*) and other species, but in the toadfish the nuclei are situated far more apically than in any of the fish studied by Woodland.

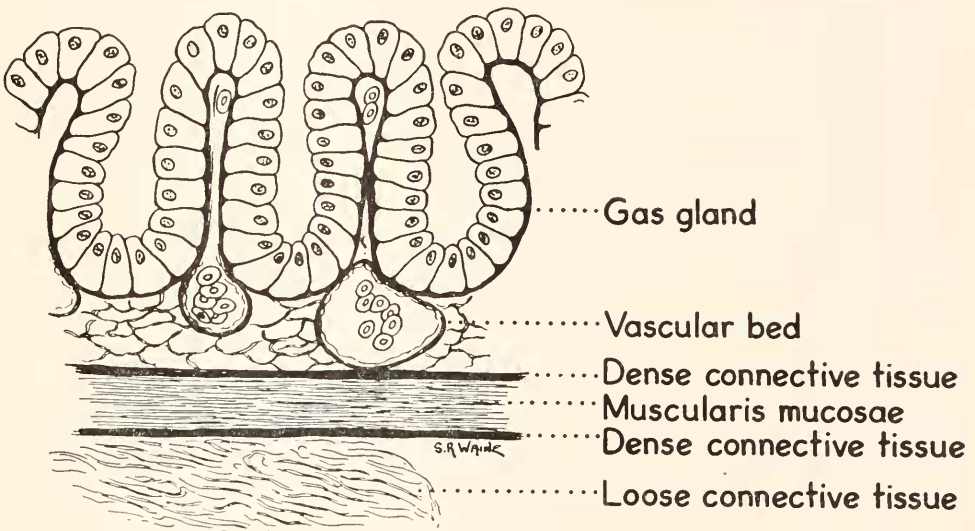


FIGURE 3. Partly diagrammatic drawing of a section through the secretory mucosa. Blood vessels are found within the folds of the secretory epithelium.

The structure of the retia mirabilia is essentially of the type described for the eel by Woodland (1911). There are 6–8 distinct retia (“red bodies”) situated in the submucosa at the junction of the floor of the anterior chamber and the diaphragm. The capillaries emanating from the retia mirabilia rejoin, to some extent, forming arterioles and venules which go to the gas gland, where they break up into capillaries providing a very rich blood supply to the glandular membrane. Every fold of the membrane contains blood vessels (Fig. 3), and it is probable that each gland cell has access to a blood capillary at its base and is separated from the blood only by a very thin endothelium. Capillary connections are found between arterioles and venules emanating from the same rete as well as between blood vessels emanating from different retia (Fig. 2).

The capillaries of a single rete mirabile were counted in a histological section. A very rough calculation indicated that the total number of capillaries of all the

retia mirabilia is 200,000–300,000, which is of the order of magnitude found by Krogh (1929) in the eel.

In the connective tissue surrounding the central parts of the retia mirabilia there are numerous nerves and ganglion cells. The ganglion cells probably give fibers to the gas gland or innervate the muscularis mucosae.

The muscularis mucosae and the diaphragm

In close connection with the inner epithelium of both the anterior and posterior chamber there is a smooth muscle layer, the muscularis mucosae. This is extremely thin in the posterior chamber but well developed in the anterior chamber, especially ventrally in connection with the glandular portion of the epithelium. The muscularis mucosae also makes a large contribution to the diaphragm where it forms a sphincter around the hole. Tower (1908) observed that the position of the diaphragm varies from about one-third of the distance from the posterior end to less than one-sixth of the distance. We have observed the same variations. That these changes of the position of the diaphragm are due to reflex movements of the muscularis mucosae is shown by the following observations: (1) In a specimen in which gas secretion had been stimulated by emptying the bladder three hours earlier, the diaphragm had a posterior position, by which consequence the anterior chamber was enlarged and the posterior chamber diminished. The hole in the diaphragm was closed. (2) In a specimen which suffered from asphyxiation and which in addition had received an injection of adrenaline (0.1 ml., 1:1000), the diaphragm was found in the anterior position and with its hole open. (Asphyxia and adrenaline each stimulate gas resorption.) (3) In individuals, where the hole in the diaphragm was initially closed, application of a small drop of adrenaline solution to the margin of the hole caused this to open to a width of 2–3 mm. It is evident that movements of the muscularis mucosae are among the physiological regulatory mechanisms which control reflexly the function of the secretory chamber (the gas gland) and the resorbent chamber ("the posterior vascular organ").

The blood supply of the swimbladder

The swimbladder receives its blood from a branch of the coeliac artery, the swimbladder artery (Fig. 1). The individual retia of the anterior chamber are supplied by branches from the swimbladder artery. Within each rete the arterial and venous capillaries form the typical counter-current exchange system studied by Woodland (1911), Haldane (1922), Krogh (1929) and Scholander (1954). All the blood to the anterior chamber passes through the retia. The entire venous return from the anterior chamber passes back through the retia and leaves the swimbladder by the swimbladder vein, which joins the portal vein (Fig. 1, ventral view).

The blood supply to the resorbent capillary network (the "posterior vascular organ") of the posterior chamber resembles that of *Fierasjer* (Emery, 1880) and the eel (Mott, 1950a, 1950b) in that the arterial blood is supplied from the swimbladder artery instead of from the intercostal arteries as in most physoclists. The venous return is to the cardinal vein system (Fig. 1, dorsal view).

DISCUSSION

The swimbladder of the toadfish is of the typical euphysoclist type (Rauther, 1922; Fänge, 1953). It shows many similarities, both physiologically and morphologically, with that of the eel.

The swimbladder of the toadfish is apparently specialized for the production of sounds (Tower, 1908), and the tunica externa forms a thick capsule enclosing both the anterior and posterior chambers. Removal of this capsule reveals the homology of the two chambers with corresponding parts of the eel swimbladder (Fig. 4). (For previous descriptions of the swimbladder of the eel see Queckett

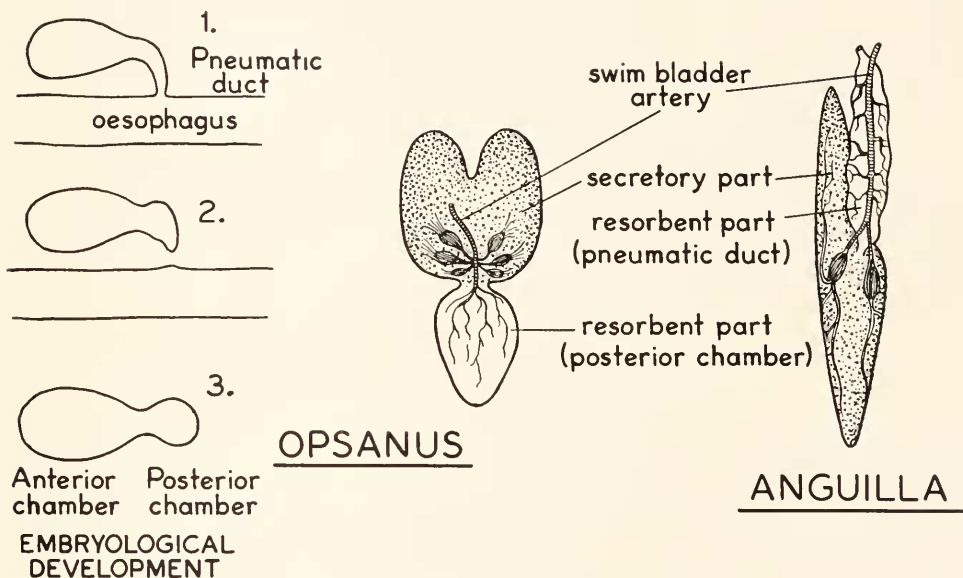


FIGURE 4. The swimbladder of the toadfish (*Opsanus tau*) and the eel (*Anguilla anguilla*) illustrating the similarity in general structure. The embryological stages to the left in the figure are redrawn from Tracy (1911). Note the transformation of the embryonic pneumatic duct into the posterior chamber.

(1844), Woodland (1911), Rauther (1922), Fänge (1953).) The anterior chamber of the toadfish swimbladder corresponds to the swimbladder *per se* in the eel and the posterior chamber corresponds to the pneumatic duct of the eel. The homology is further substantiated by the embryonic development of the toadfish swimbladder (Tracy, 1911) during which the posterior chamber develops from the embryonic pneumatic duct. The muscularis mucosae of the toadfish and the eel respond to adrenaline in a similar manner; the anterior chamber of the toadfish swimbladder and the swimbladder of the eel both are contracted by adrenaline while the posterior chamber of the toadfish swimbladder and the pneumatic duct of the eel are relaxed (Fänge, 1953).

Woodland (1911), in his classic description of the gas gland, distinguishes three major types of gas glands: those in which the glandular epithelium is composed

of a single layer of cells, those in which the gland is massive, and those in which a primitively single layer of cells is secondarily folded into a massive structure. The toadfish, in common with the eel, belongs to the first category (Woodland, 1911) in which (p. 193) "the glandular epithelium is composed of a single layer of cells which either remains unfolded or is only simply folded. . . ." Microscopically, according to our present observations, the glandular epithelia of the toadfish and the eel swimbladder are scarcely distinguishable in appearance. Woodland further subdivides his first class of gas glands on the basis of the extent of the glandular epithelium and the degree of reunion of the blood vessels. The toadfish belongs to the Syngnathus subdivision, type Ib, in which (p. 195) "the glandular epithelium is restricted in area, not lining the whole of the bladder cavity, and the rete mirabile is contiguous with the gas gland, although a small amount of reunion of the capillaries of the rete may occur before these supply the epithelium."

The gas mixtures secreted into the swimbladders of the toadfish and the eel are markedly similar (Wittenberg, unpublished data; Wittenberg, 1958). The oxygen content is very high, up to 95 per cent, and the carbon dioxide content usually is low, about 4 per cent. The ratio of argon to nitrogen is very high and approaches what may be a theoretical maximal value, 2.6×10^{-2} (Wittenberg, 1958). Both the toadfish and the eel possess highly efficient, powerfully developed, oxygen transporting mechanisms, obviously of very similar nature.

SUMMARY

1. The anatomy of the swimbladder and the gas gland of the toadfish (*Opsanus tau* L.) is described. The swimbladder is of the euphysoclist type. The gas gland is composed of a single cell layer.

2. Both physiologically and morphologically the swimbladder of the toadfish shows strong resemblances to that of the eel (*Anguilla*). The swimbladder normally has a high proportion of oxygen, an unusual feature for fishes living in shallow water.

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